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The taxonomic status of the vipers of the *Pelias* (*kaznakovi*) complex in the middle-flow of the Kura River basin in the East Transcaucasia

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ABSTRACT

Recently, the Caucasian viper was found in a number of localities in South Ossetia (Tuniyev et al. 2017a,b; Tuniyev et al. 2019) and in the lower gate of the Borzhom Gorge of Eastern Georgia. Animals from the new localities are compared to *Pelias kaznakovi* from the Western Caucasus – northeastern Turkey and *P. dinniki*. The canonical discriminate analysis (CDA) showed that the snakes from the left-bank basin of the middle flow of the Kura River in East Georgia and South Ossetia differ significantly from *Pelias kaznakovi* from Krasnodar Territory and Abkhazia in the mean values of several plastic and meristic characters. Thus, there is discrimination of the groups allocated according to geographic location and gender. Cluster analysis based on meristic characters of pholidosis showed the distance between *P. dinniki* and the remaining "*kaznakovi*" complex forms. Based on the results of the analysis of the mitochondrial cytochrome *b* gene, the snakes from the left-bank basin of the middle flow of the Kura River form a separate cluster, not sister to *Pelias kaznakovi*. The results obtained on morphology, genetics and ecology of the studied vipers suggest the taxonomic validity of the vipers from the left bank basin of the middle flow of the Kura River in Eastern Georgia and South Ossetia. The species is named after Boris Tuniyev, who made a significant contribution to the study of the Caucasian herpetofauna and taxonomy of the shield-head viper snakes. Among the representatives of the "*kaznakovi*" complex, males of the new species are characterized by the minimal values of body length, pileus length, head width, number of ventral and subcaudal shields, as well as the shields around the eyes; differences are also noted in the structure of the hemipenis; the females have the minimum values of body length, pileus length, head width, number of shields around the eyes and loreals, fewer wings of zigzag. All known finds are located in the left bank basin of the middle flow of the Kura River from the Borzhom Gorge (east slope of Meskheti Ridge) in Georgia to the mid-altitude mountain districts of South Ossetia (east foothills of Likhsky Ridge and south spurs of Central Caucasus). Biotopes of the new species are characterized by more xero-mesophilic traits and a moderately warm mezo-climate than the typical mesophilic biotopes of North-Colchian (Krasnodar Territory – Abkhazia) and, especially, Adzharo-Lazistanian (Georgia – Turkey) *P. kaznakovi* living in the humid subtropical climate.

Key words: East Transcaucasia, new species, *Pelias tuniyevi*, viperid snakes

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Таксономический статус гадюк *Pelias* (*kaznakovi*) комплекса из бассейна среднего течения реки Кура в Восточном Закавказье

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РЕЗЮМЕ

Сравнительно недавно кавказская гадюка была найдена в ряде локалитетов Южной Осетии (Туниев и др. 2017a,b; Tuniyev et al. 2019) и в нижнем створе Боржомского ущелья Восточной Грузии. Животные из новых локалитетов сравнены с *Pelias kaznakovi* из Западного Закавказья – северо-восточной Турции и *P. dinniki*. Обнаружены существенные отличия в средних значениях ряда пластических и меристических признаков змей из левобережного бассейна среднего течения р. Кура в Восточной Грузии и Южной Осетии, в сравнении с *Pelias kaznakovi* из Краснодарского края и Абхазии, а также дискриминация групп, выделенных по принципу географической и половой принадлежности, в ходе дискриминантного анализа. Кластерный анализ по совокупности признаков фолидоза показал дистанцированность между *P. dinniki* и остальными формами «*kaznakov*i» комплекса. По результатам анализа митохондриального гена цитохрома *b*, гадюки из левобережного бассейна среднего течения р. Кура формируют отдельный кластер, не сестринский по отношению к *Pelias kaznakovi*. Базируясь на морфологических и молекулярных результатах, особенностях экологии, животные из левобережного бассейна р. Кура в Восточной Грузии и Южной Осетии, на наш взгляд, заслуживают статус самостоятельного вида. Вид назван в честь Бориса Туниева, внесшего значительный вклад в изучение герпетофауны Кавказа и таксономии щиткоголовых гадюковых змей. Среди представителей «*kaznakovi*»-комплекса самцы нового вида имеют минимальные значения длины тела, пилеуса, ширины головы, количества вентральных и подхвостовых щитков, а также щитков вокруг глаз; отмечены отличия и в строении гемипениса. Самки имеют минимальные значения длины тела, пилеуса, ширины головы, количества щитков вокруг глаз и скуловых щитков, меньшее количество петель зигзага. Все известные находки приурочены к левобережному бассейну среднего течения р. Кура от Боржомского ущелья (восточный склон Месхетского хребта) в Грузии до среднегорных р-нов Южной Осетии (восточные предгорья Лихского хребта и южные отроги Центрального Кавказа). Биотопы нового вида характеризуются более ксеромезофильными чертами и умеренно-теплым мезоклиматом, чем типичные мезофильные биотопы северо-колхидских (Краснодарский край – Абхазия) и, особенно, аджаро-лазистанских (Грузия – Турция) *P. kaznakovi,* обитающих в условиях влажного субтропического климата.

Ключевые слова: Восточное Закавказье, новый вид, *Pelias tuniyevi*, близкие виды гадюк

INTRODUCTION

The geographic range of the Caucasian viper *Pelias kaznakovi* (Nikolsky, 1909) was considered as two clusters: North-Colchis (Krasnodar Territory, Adygei, Abkhazia and Western Georgia) and Adzharo-Lazistan (Adzharia and northeastern Turkey) (Orlov and Tuniyev 1986; Tuniyev 2016; Tuniyev et al. 2019), with the latest clarifications for the south-eastern, Turkish, part of the range in the Chorokh River basin, on the Lazistan Coast (Afsar and Afsar 2009; Mebert et al. 2015, 2016) and Krasnodar Territory, northwest part of the range (Tuniyev 2016; Tuniyev and Tuniyev 2017). The find of M.A. Bakradze (1969) was the only record of the species in the Eastern Transcaucasia in the Baniskhevi River Gorge (side offshoot of the Borzhom Gorge, left tributary of the Kura River in Georgia), the reference, which was used in all subsequent literature. Relatively recently, the Caucasian viper was found in a number of localities in South Ossetia (Tuniyev et al. 2017b; Tuniyev et al. 2019) and by G.N. Iremashvili in the lower gate of the Borzhom Gorge.

In the left-bank basin of the middle flow of the Kura River, vipers undoubtedly belong to the "*kaznakovi*" complex, but they differed from the typical *P. kaznakovi* living in the Western Caucasus and in the Adzharo-Lazistan part of the range by the elements of coloration, as well as dimensional characteristics and ecology. We compare the vipers from the left-bank basin of the Kura River with vipers from the northern part of the Western Transcaucasia, including a specimen from the type territory of *P. kaznakovi* (Tsebelda, Abkhazia), and the southwestern Transcaucasia [Adzharia (Georgia) and Turkey].

Institutional and other abbreviations. Ab – Abkhazia; Ge – Georgia; KT – Krasnodar Territory, Russia; SNP – Herpetological collection of the Sochi National Park, Sochi, Russia; SO – South Ossetia; ZISP – Zoological Institute of the Russian Academy of Sciences, Saint Petersburg, Russia; Mt. – Mountain; V. – Village; asl – above sea level.

MATERIALS AND METHODS

The material was collected in 2014–2019 during expeditions in SO and Ge. 124 specimens of vipers related to the "*kaznakovi*"-complex from Western Transcaucasia, Eastern Ge, SO, south-west Ge (Adzharia) and highlands of West Caucasus were used in statistical, cluster and discriminant analyses (Table 1). Most of the material was collected personally by B.S. Tuniyev and/or during his expeditions of Sochi National Park. Specimens collected are stored in SNP. The comparative analysis involves also specimens stored in the ZISP (Table 1).

Pregnant females were kept in a standard terrarium to birth of juveniles, which provided additional material on pholidosis and reproductive biology. Additional published data on morphology of *P. kaznakovi* from Turkey (Baran et al. 2005; Afsar and Afsar 2009; Gül et al. 2016) were considered in the analysis. Comparison of color patterns of vipers from the Adzharo-Lazistan part of the geographic range was made from photos, courtesy of B. Heras.

For the analysis of the level of genetic differentiation in cytochrome *b* (cyt*b*) based on p-distances, snakes were united into four geographical samples: 1. *Pelias* sp. (SO and Eastern Ge), 2. *P. kaznakovi* (KT), 3. *P. dinniki* "west" (West Caucasus: Ab, KT, Adygei, Karachay-Cherkessia), 4. *P. dinniki* "east" (Central Caucasus: SO, North Ossetia-Alania).

Methods of traditional morphology were used for morphological characters provided by Nilson and Andrén (2001), with our modification (Table 2). All measurements were made by B.S. Tuniyev. To eliminate the effect of age variation, comparison of adult and juvenile males and females was made separately only for the meristic characters. Samples 1–3 were studied statistically using standard methods of variation statistics (Lakin 1990) and one of the methods of multidimensional statistics – Canonical Discriminate Analysis (CDA), and cluster analysis (Tyurin et al. 2003) using STATISTICA 6.0 for Windows. Statistical, cluster and canonical analyses used data on 114 adult and immature specimens of vipers. Data for the fourth sample will be presented in a separate publication.

NA extraction, amplification and sequencing

29 specimens sampled at 16 localities (Fig. 1, Table 3) were used in the current study, additionally three sequences were taken from GenBank (KC176731, JX114025 and KJ415303) and eight sequences of *P. shemakhensis* and *P. renardi* were published in our previous study (Tuniyev et al. 2018). Genomic DNA was isolated from tissues fixed with 96% ethanol using standard salt extraction protocol (Miller et al. 1988). A segment (1154 bp) of cyt*b* gene

Table 1. Examined specimens of Pelias spp. See text for abbreviation

No	Species	n	Sample	Collection locality	Date	Collector
SNP 500	*P. kaznakovi*	2	2	Maliy Kichmay V., KT	06.1994	Filippov V.I.
SNP 716	*P. kaznakovi*	1	2	Maliy Kichmay V., KT	09.2006	Tuniyev B.S.
SNP 512	*P. kaznakovi*	5	2	Maliy Kichmay V., KT	31.05.1996	Tuniyev B.S., Tuniyev S.B.
SNP 502	*P. kaznakovi*	4	2	Maliy Kichmay V., KT	1995	Kornilov A.
SNP 1083	*P. kaznakovi*	1	2	Amuko Mt., KT	18.08.2016	Suvorov A.V.
SNP 1453	*P. kaznakovi*	1	2	Tsebelda V., Ab	07.05.2019	Aliev Kh.U.
SNP 978	*P. kaznakovi*	1	2	Blagodatnaya Mt., KT	10.04.2008	Tuniyev S.B.
SNP 587	*P. kaznakovi*	1	2	Aibga V., KT	26.08.2002	Tuniyev B.S.
SNP 585	*P. kaznakovi*	1	2	Rudovaya River, KT	07.2002	Tuniyev B.S.
SNP 916	*P. kaznakovi*	8	2	Mosya Mt., KT	28.08.2012	Bykovsky S.I.
SNP 851	*P. kaznakovi*	1	2	Achishkho Mt., KT	22.06.2009	Kidov A.A.
SNP 790	*P. kaznakovi*	1	2	Zapadny Dagomys River, KT	21.07.2009	Romanov D.S.
SNP 796	*P. kaznakovi*	1	2	Adler, KT	2008	Starkov V.G.
SNP 588	*P. kaznakovi*	4	2	Aibga V., KT	26.08.2002	Tuniyev B.S.
SNP 1173	*P. kaznakovi*	1	2	Aibga V., KT	08.07.2020	Tuniyev B.S.
SNP 490	*P. kaznakovi*	1	2	Uch-Dere V., KT	07.1995	Ashalyan A.
SNP 825	*P. kaznakovi*	1	2	Achishkho Mt., KT	08.2008	Kidov A.A.
SNP 1172	*P. kaznakovi*	1	2	Aibga V., KT	08.07.2020	Minosyan V.O.
SNP 928	*P. kaznakovi*	1	2	Zubova Schel V., KT	05.2014	Tuniyev B.S.
SNP 795	*P. kaznakovi*	9	2	Achishkho Mt., KT	08.2008	Kidov A.A.
SNP 1085	*P. kaznakovi*	3	2	Amuko Mt., KT	09.2016	Suvorov A.V.
SNP 511	*P. kaznakovi*	1	2	Orlinye Skaly, KT	11.05.1996	Tuniyev B.S., Tuniyev S.B.
SNP 754	*P. kaznakovi*	1	2	Blagodatnaya Mt., KT	10.04.2008	Tuniyev B.S.
SNP 496	*P. kaznakovi*	1	2	Matsesta, KT	05.1935	Lychagov A.V.
SNP 759	*P. kaznakovi*	1	2	Soutlyantepe Mt., KT	10.04.2008	Tuniyev B.S.
SNP 1089	*P. kaznakovi*	1	2	Khakukay Mt., KT	03.05.2017	Minosyan V.O.
SNP 1078	*P. kaznakovi*	1	2	Aibga V., KT	14.09.2016	Minosyan V.O.
SNP 1084	*P. kaznakovi*	7	2	Amuko Mt., KT	09.2016	Tuniyev B.S.
SNP 586	*P. kaznakovi*	2	2	Rudovaya River, KT	08.2002	Tuniyev B.S.
SNP 791	*P. kaznakovi*	1	2	Tretya Rota V., KT	21.07.2009	Romanov D.S.
SNP 594	*P. kaznakovi*	1	2	Kashtany V., KT	09.2002	Lebedeva A.A.

No	Species	n	Sample	Collection locality	Date	Collector
SNP 789	*P. kaznakovi*	1	2	Amuko Mt., KT	13.07.2009	Tuniyev B.S.
SNP 1060*	*P. kaznakovi*	1	–	Mtirala Mt., Ge	08.05.2016	Tuniyev B.S.
SNP 941*	*P. kaznakovi*	1	–	Kintrish River, Ge	2005	Iremashvili G.N.
SNP 1141*	*P. kaznakovi*	1	-	Kintrish River, Ge	08.05.2018	Elbanidze G.
SNP 937	*Pelias sp.*	1	1	Kharisdzhin V., SO	14.05.2014	Khasity G.V.
SNP 1182	*Pelias sp.*	1	1	Kharisdzhin V., SO	14.05.2014	Khasity G.V.
SNP 1140	*Pelias sp.*	1	1	Tashiskari V., Ge	22.07.2017	Iremashvili G.N.
SNP 1086	*Pelias sp.*	1	1	Atsriskhevi V., SO	18.08.2016	Tikhonov V.V.
SNP 1054	*Pelias sp.*	8	1	Tashiskari V., Ge	09.2015	Khachidze Z.
SNP 951	*Pelias sp.*	1	1	Kharisdzhin V., SO	14.05.2014	Khasity G.V.
SNP 1935	*Pelias sp.*	1	1	Uanat V., SO	03.09.2018	Bukulov Ch.B.
SNP 1095	*Pelias sp.*	1	1	Atsriskhevi V., SO	07.09.2019	Tikhonov V.V.
SNP 1079	*Pelias sp.*	1	1	Atsriskhevi V., SO	18.08.2016	Tikhonov V.V.
SNP 930	*Pelias sp.*	1	1	Gufta V., SO	05.08.2019	Gabaev V.N.
SNP 936	*Pelias sp.*	1	1	Kharisdzhin V., SO	23.04.2014	Khasity G.V.
SNP 915	*Pelias sp.*	1	1	Atsriskhevi V., SO	23.09.2012	Komarov Yu.E.
SNP 646	*P. dinniki*	16	3	Kardyvach Lake, KT	25.07.2004	Tuniyev S.B.
SNP 592	*P. dinniki*	2	3	Chugush Mt., KT	07.2000	Tuniyev B.S.
SNP 647	*P. dinniki*	1	3	Buynaya River (Mzymta River basin), KT	04.07.2004	Tuniyev S.B.
SNP 627	*P. dinniki*	1	3	Kamenny Klad Ridge, Ab	30.08.2004	Tuniyev S.B.
SNP 628	*P. dinniki*	1	3	Kamenny Klad Ridge, Ab	30.08.2004	Tuniyev S.B.
SNP 652	*P. dinniki*	1	3	Kamenny Klad Ridge, Ab	30.08.2004	Tuniyev S.B.
ZISP 22306	*P. dinniki*	2	3	Fisht-Oshten Mt. Massive, Adygei, Russia	08.1990	–
SNP 650	*P. dinniki*	1	3	Armyansky Pass, Adygei, Russia	20.07.2004	Tuniyev S.B.
SNP 630	*P. dinniki*	1	3	Khakudzh Mt., KT	20.09.2004	Tuniyev S.B.
SNP 655	*P. dinniki*	1	3	Khakudzh Mt., KT	20.09.2004	Tuniyev S.B.
SNP 656	*P. dinniki*	1	3	Khakudzh Mt., KT	20.09.2004	Tuniyev S.B.
SNP 590	*P. dinniki*	2	3	Yukha Mt., Karachay-Cherkessia, Russia	06.2001	Tuniyev B.S.
SNP 591	*P. dinniki*	3	3	Yukha Mt., Karachay-Cherkessia, Russia	06.2001	Tuniyev B.S.
SNP 582	*P. dinniki*	1	3	Chistaya River, Adygei, Russia	07.2002	Nikitin V.V.
SNP 715	*P. dinniki*	1	3	Pikhtovaya glade on Psekhako Ridge, KT		Tuniyev S.B.

Note: * – specimens considered in the analysis of morphometric characters, but due to the limited number not included in the statistical analysis

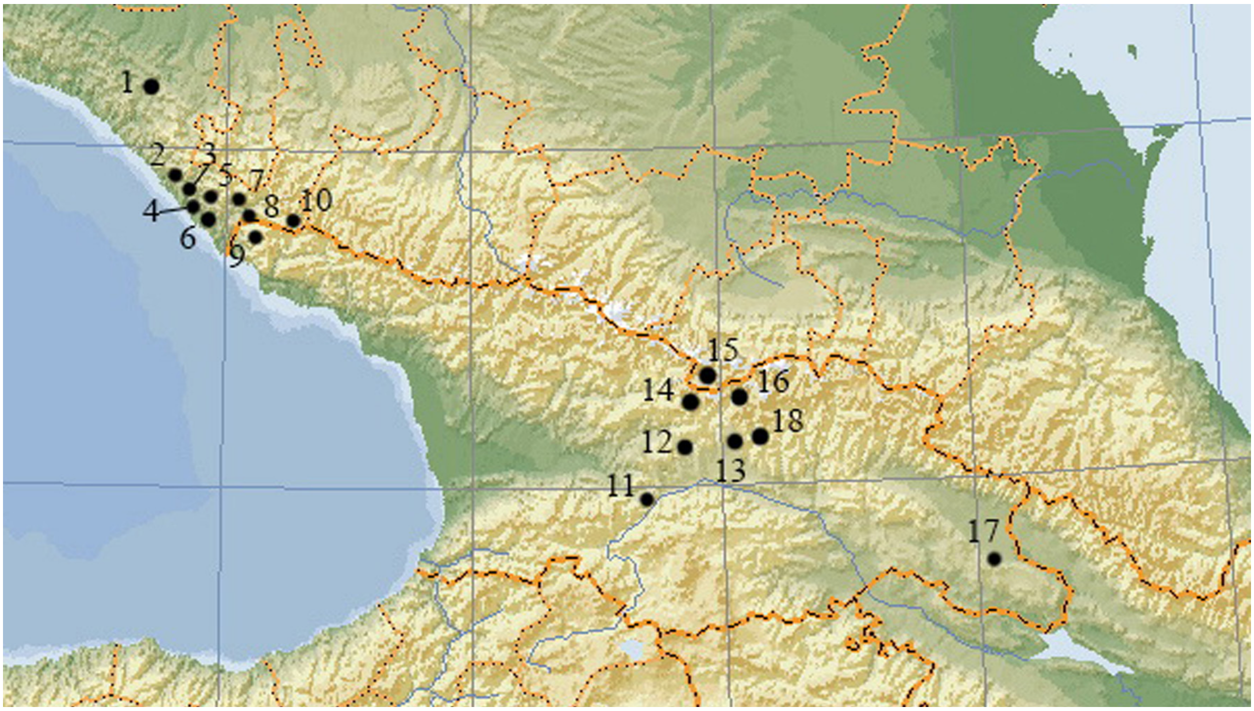


Fig. 1. The localities of sampling on the Pelias spp. for the genetic analysis: 1. Saratovskaya Settlement, KT. 2. Mt. Blagodatnaya, KT. 3. Mt. Soutlyantepe, KT. 4. Maliy Kichmay V., KT. 5. Mt. Amuko, KT. 6. Mt. Mosya, KT. 7. Mt. Achishkho, KT. 8. Aibga V., KT. 9. Kamenny Klad Ridge, Ab. 10. Kardyvach Lake, KT. 11. Tashiskari V., Ge. 12. Kharisdzhin V., SO. 13. Uanat V., SO. 14. Dzhodzhora River, SO. 15. Zrug Gorge, North Ossetia-Alania, Russia. 16. Cheliatdon River, SO. 17. Vicinity of Chinkani V. and Khornabudji castle, Ge. 18. Vicinity of Atsriskhevi V. ruins, SO.

was amplified using primers Cyt*b*_F1 and Cyt*b*_RC, additional internal primer Cytb_F8 was used for sequencing (Stumpel 2012). PCR conditions were as published in Zinenko et al. (2015), each PCR included a negative control. The PCR products were purified on columns of an Omnix kit (Omnix, Saint Petersburg, Russia) and sequenced in both directions. Sequences were edited and assembled using BioEdit (Hall 1999). All sequences received as part of this work were uploaded to the GenBank under the numbers MW246030-MW246058.

Phylogenetic analyses

Tree reconstructions were performed using 38 specimens of *Pelias* spp. *Bitis arietans* (Merrem 1820) (JX114025) and *Montivipera xanthina* (Gray 1849) (KJ415303) were used as outgroup. The final alignment comprised the 686 bp *cytb* fragment. Phylogenies were reconstructed using Bayesian inference (BI) and maximum likelihood (ML) approaches. BI analysis was performed in MRBAYES 3.2.2 (Ronquist and Huelsenbeck 2003). Each BI analysis started with random trees and performed two independent runs with four Markov chains Monte Carlo (MCMC) for 2 million generations with sampling every 1000th generation under nst=mixed, rates=gamma. Consensus trees constructed based on the trees sampled after the 25% burn-in. The best model of molecular evolution (TN:G:5) was chosen and ML analysis was calculated with TREEFINDER (Jobb 2011). Bootstrap analysis employed 1000 replicates. Final trees obtained in FIGTREE v1.4.0 (http://tree.bio.ed.ac.uk/software/figtree/). The level of genetic differentiation in *cytb* based on p-distances was estimated in Mega 7 (Kumar et al. 2016).

RESULTS OF THE ANALYSES

1. Morphological characters

Morphological characteristics of vipers from the populations studied are presented in Tables 4–9. Vipers from the left-bank basin of the Kura River (T.l. ♂♂ – 421.3; ♀♀ – 412.5) are much smaller than

Table 2. Abbreviation for morphological characters and indexes of vipers

No	Abbreviation	**Description**
1	T.l.	Total length
2	SVL.	Snout-vent length
3	L.cd.	Distance from cloaca to tail tip
4	Pr.	Number of preventral shields
5	Ven.	Number of ventral shields
6	S.c.	Number of subcaudal shields
7	Ap.	Number of apical shields
8	R.	Rostral index: ratio of height to width
9	Pil.	Distance from tip of snout to posterior margin of parietals shields
10	Crown scales (C.s.)	Number of shields, limited by frontals, canthals and supraoculars
11	In	Upper preocular in contact with nasal, left/right (+/-)
12	Can.	Number of canthal shields
13	Sq.1	Number of dorsal scales around the neck
14	Sq.2	Number of dorsal scales around midbody
15	Sq.3	Number of dorsal scales around posterior part of body
16	Supralab	Number of supralabial shields
17	Sublab	Number of sublabial shields
18	F.c.	Number of shields round eye (left/right)
19	ZZ	Number of zigzag windings (left/right)
20	Lor.	Number of loreal shields (left/right)
21	L.c.	Head length
22	Lt.c	Biggest width of head
23	Al.c.	Height of head in parietal area
24	Par.	Parietals (hel/delad)
25	Front.	Frontal (hel/delad)
26	Nas.	Nasal (hel/delad)

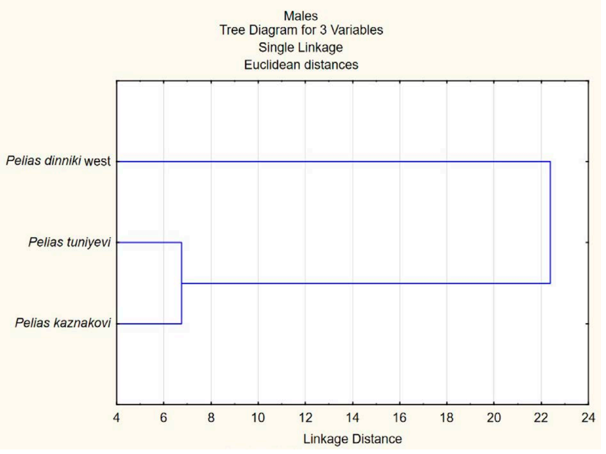


Fig. 2. Results of the cluster analysis (UPGMA method) of three groups of males of Pelias spp. based on pholidosis characters

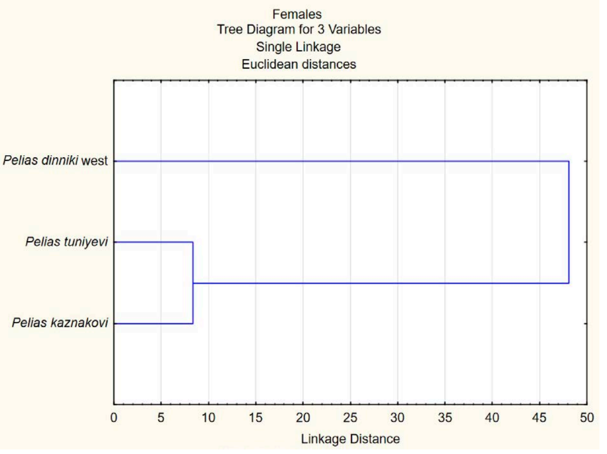


Fig. 3. Results of the cluster analysis (UPGMA method) of three groups of females of Pelias spp. based on pholidosis characters

vipers from KT Ab (T.l. ♂♂ 443.0; ♀♀ 467.4) and Adzharia Lazistan (T.l. ♂♂ – 489.3; ♀♀ – 492.3). The pileus (Pil) of males and females from the Kura River basin (♂♂ – 12.5; ♀♀ – 12.0) is shorter than in vipers from KT – Ab (♂♂ – 13.5; ♀♀ – 13.4). Vipers from the northern part of the Western Transcaucasia have a much broader head (Lt. c.), which makes their rostral index (R) significantly lower (♂♂– 61.6; ♀♀ – 61.2) than in the vipers from the Kura River basin (♂♂ – 72.6; ♀♀ – 68.3).

Based on the results of the comparison of meristic characters between samples, we found the following differences (Tables 10–11).

Comparison of meristic characteristics of males of all age groups showed diminishing of the number of ventral scales (Ven) in vipers of the Kura River basin (129.3) compared to the vipers from KT – Ab (131.2) and Adzharia – Lazistan (130.8). Similarly, the number of sub-tail shields (S.cd) is lower in males from the Kura River basin (31.8) than in males from the northern part of the Western Transcaucasia (35.5) and Adzharia – Lazistan (34.5). Males from the Kura River basin showed a fewer shield number around their eyes (F.c) (19.3) than males from the northern part of the Western Transcaucasia (21.5), but almost equal to vipers from Adzharia – Lazistan (19.5).

Generalizing the data on the size and external morphology of males, we can state that vipers from the left bank basin of the middle flow of the Kura River are characterized by the minimal values of body length, pileus length, head width, number of ventral and subcaudal shields, as well as the shields around the eyes.

Comparison of meristic characteristics of females of all age groups showed similar diminishing of the number of ventral scales (Ven) in vipers of the Kura River basin (133.1) compared to the vipers from KT – Ab (135.3) and Adzharia – Lazistan (135.8), but these differences were statistically insignificant.

Similarly insignificant were the differences in the number of subcaudals (S.cd.), which are fever in the females from the Kura River basin (25.6) than the vipers from KT Ab (27.2) and Adzharia – Lazistan (25.3).

Statistically significant differences were noted in the number of shields around the eyes (F.c.): females from the Kura River basin (18.6) had fewer shields than females from the KT – Ab (20.8), and the vipers from the Adzharo-Lazistan population (19.5). The number of loreals (Lor.) was minimal in females from the Kura River basin (8.7), but maximal in females from KT – Ab (11.0). A higher number of loreals (11.3) was also noted in the specimens from Adzharia – Lazistan.

The minimal number of wings of zigzag was recorded in females from the Kura River basin (114.9), the maximum value was from the KT – Ab (123.5).

Generalizing the material on the external morphology of females, we can state that the minimum values of body length, pileus length, head width, number of shields around the eyes and loreals, and fewer wings of zigzag were observed in the vipers from the populations of the Kura River basin.

Table 3. Specimens of *Pelias* spp. used for the analysis of mitochondrial cyt *b*. Voucher specimens are stored in SNP. For localities information (numbers in brackets), see Fig. 1

Species	Tissue No.	Genbank accession No.	Locality	Voucher No.
P. kaznakovi	113	MW246049	Blagodatnaya Mt., KT (2)	754
	115	MW246050		756
	114	MW246054	Soutlyantepe Mt., KT (3)	759
	120	MW246053	Maliy Kichmay V., KT (4)	716
	111	MW246058	Amuko Mt., KT (5)	789
	426	MW246057		1083
	230	MW246051	Mosya Mt., KT (6)	916
	382	MW246052		1000
	119	MW246055	Achishkho Mt., KT (7)	825
	425	MW246056	Aibga V., KT (8)	1078
P. dinniki "west"	326	MW246041	Kamenny Klad Ridge, Ab (9)	973
	327	MW246042		973
	328	MW246045		973
	380	MW246046		998
	381	MW246047		999
	131	MW246048	Kardyvach Lake, KT (10)	921
P. dinniki "east"	437	MW246040	Dzhodzhora River, SO (14)	1097
	244	MW246043	Zrug Gorge, North Ossetia-Alania, Russia (15)	958
	245	MW246044		958
	275	MW246037	Cheliatdon River, SO (16)	956
	276	MW246038		956
	277	MW246039		956
Pelias sp.	406	MW246034	Tashiskhari V., Ge (11)	1054
	407	MW246035		1054
	411	MW246036		1054
	246	MW246032	Kharisdzhin V., SO (12)	937
	249	MW246031		936
	248	MW246030	Uanat V., SO (13)	935
	427	MW246033	Atsriskhevi V., SO (18)	1086

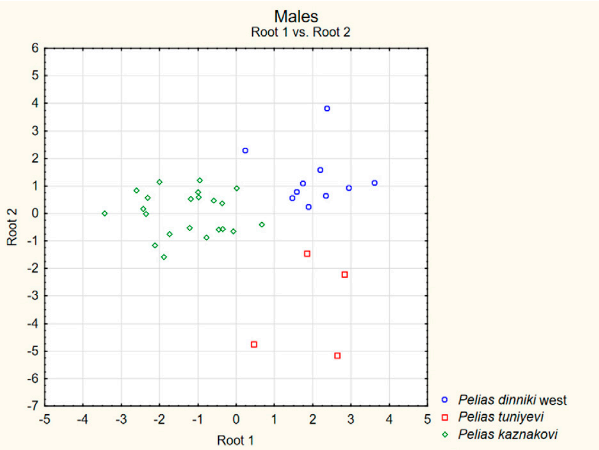


Fig. 4. Two-dimensional scatterplot of samples of males of the steppe vipers in space of CDA function on the complex of morphometric characters

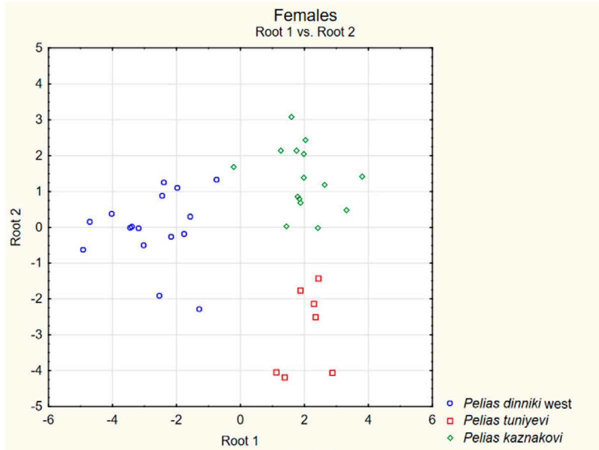


Fig. 5. Two-dimensional scatterplot of samples of females of the steppe vipers in space of CDA function on the complex of morphometric characters

Vipers of both sexes from the Kura River basin differed from all other vipers being compared in the small sizes and the minimal number of shields around the eyes.

Due to the heterogeneity and a low number of individual samples, as well as individual population variability, sexual dimorphism in the populations studied was studied for each population separately (Tables 4–8):

Pelias sp., left bank of the Kura River basin (n=11). The length of the tail and the number of subcaudals is higher in males, while the number of ventrals is higher in females than in males.

Pelias kaznakovi, KT – Ab (n=67). The body length, the length and width of the head and the number of ventrals are higher in females, while the length of the tail and the number of subcaudals are higher in males than in females. Similar results were obtained for *P. kaznakovi* from Adzharia – Lazistan (n=10).

Pelias dinniki, West Caucasus (n=35). The length of the tail and the number of subcaudals are higher in males. Around the middle of the body, the number of scales in females is higher than in males.

The cluster analysis of both sexes resulted in a dendrogram based on 14 meristic characters of pholidosis forming two big clusters: the first division occurs between *P. dinniki* and all other forms, with subsequent splitting of the latter into two separate clusters (Figs 2, 3).

The geographical variability of morphological characters in investigated populations of vipers was considered also with the use of CDA, allowing a comparison of the preliminary selected groups in the complex of characters (Tyurin et al. 2003). For comparison, *P. dinniki* was taken as an outgroup.

We used a complex of fourteen meristic characters (Pr., Ven., S.cd., Ap., Can., C.s., Sq.1, Sq.2, Sq.3, Supralab., Sublab., ZZ., F.c., Lor.) for which the reliable differences were obtained in the statistical analysis. The vipers were divided a priori into six groups based on criteria of gender and geographic location.

The results of CDA showed the absolute accuracy of the division of the geographical groups. The accuracy for the males and females are the following: west *Pelias dinniki* – 100%, *P. kaznakovi* (KT – Ab) – 100%, *Pelias* sp. (Kura River) – 100%.

The results of CDA showed that in the space of discriminant functions the males formed three groups without overlapping the clouds (Fig. 4): 1) *P. dinniki* "*west*"; 2) *P. kaznakovi* from KT – Ab; 3) *P.* sp. from left bank basin of the middle flow of the Kura River. In both discriminant functions, the animals were divided into two groups.

The distribution of the females in the space of discriminant functions (Fig. 5) looks also heterogeneous with the formation of three independent groups without overlapping the clouds. Like males, females in both discriminant functions were divided into two groups.

The results obtained confirm a high degree of morphological separation of the compared samples of vipers. The degree of likeness between the selected

Table 4. Comparison of morphological characters of adult and juvenile specimens of *Pelias tuniyevi* sp. nov. from SO – Ge. See Table 2 for abbreviations

Character	♂♂ Adults (n = 3) min–max X̄±m	♂♂ Juv. (n = 1) min–max X̄±m	♀♀ Adults (n = 6) min–max X̄±m	♀♀ Juv. (n = 3) min–max X̄±m	♂♂ Adults + Juv. (n = 4) min–max X̄±m	♀♀ Adults + Juv. (n = 9) min–max X̄±m	t	p
T.l.	382–471 421.3 ± 26.2	156	327–466 412.5 ± 20.2	171–205 190.3 ± 10.1	–	–	–	–
SVL	330–401 365.3 ± 20.5	136	297–425 371.7 ± 18.4	149–185 169.7 ± 10.7	–	–	–	–
L.cd	46–70 56 ± 7.2	20	30–46 40.8 ± 2.4	20–22 20.7 ± 0.7	–	–	–	–
Pil	12–13.4 12.5 ± 0.5	8.8	10.6–13.2 12 ± 0.5	7.7–9.7 8.7 ± 0.6	–	–	–	–
L.c.	20.7–22.9 21.5 ± 0.7	13.0	20.3–22.7 21.6 ± 0.4	13.4–16.2 14.4 ± 0.9	–	–	–	–
Lt.c.	11.3–12.3 11.8 ± 0.3	8.2	11.1–14.4 12.5 ± 0.5	7.6–9.6 8.3 ± 0.7	–	–	–	–
Al.c	7.9–9.3 8.6 ± 0.4	4.9	7–10 8.5 ± 0.5	5–6.9 5.7 ± 0.6	–	–	–	–
R	69.9–75.6 72.6 ± 1.7	59.76	56.9–90.1 68.3 ± 5.1	65.8–71.9 68.7 ± 1.8	–	–	–	–
Pr	2–3 2.7 ± 0.3	1	1–4 2.3 ± 0.4	1–3 2 ± 0.6	1–3 2.3 ± 0.5	1–4 2.2 ± 0.3	0.04	>0.05
Ven	128–131 129.7 ± 0.9	128	129–136 132 ± 1	130–139 135.3 ± 2.7	128–131 129.3 ± 0.8	129–139 133.1 ± 1.2	**2.45**	<0.05
S.cd.	28–36 33 ± 2.5	28	23–28 24.8 ± 0.7	25–31 27 ± 2	28–36 31.8 ± 2.2	23–31 25.6 ± 0.8	**3.34**	<0.01
Ap	1–2 1.3 ± 0.3	1	1–2 1.3 ± 0.2	1–2 1.7 ± 0.3	1–2 1.3 ± 0.3	1–2 1.4 ± 0.2	0.62	>0.05
C.s.	5–14 8.7 ± 2.7	5	4–9 7.2 ± 0.8	6–14 10.7 ± 2.4	5–14 7.8 ± 2.1	4–14 8.3 ± 1	0.28	>0.05
Can	5–7 6 ± 0.6	5	5–7 5.7 ± 0.3	5–6 5.7 ± 0.3	5–7 5.8 ± 0.5	5–7 5.7 ± 0.2	0.18	>0.05
Sq1	21–23 21.7 ± 0.7	21	20–22 20.8 ± 0.3	21–23 22.3 ± 0.7	21–23 21.5 ± 0.5	20–23 21.3 ± 0.4	0.25	>0.05
Sq2	21–22 21.3 ± 0.3	21	19–21 20.7 ± 0.3	21–22 21.3 ± 0.3	21–22 21.3 ± 0.3	19–22 20.9 ± 0.3	0.84	>0.05
Sq3	17–19 17.7 ± 0.7	16	16–17 16.8 ± 0.2	17–17 17 ± 0	16–19 17.3 ± 0.6	16–17 16.9 ± 0.1	0.84	>0.05
Supralab	16–19 17.7 ± 0.9	20	18–19 18.3 ± 0.2	16–18 17.3 ± 0.7	16–20 18.3 ± 0.9	16–19 18 ± 0.3	0.36	>0.05
Sublab	19–21 19.7 ± 0.7	20	19–22 21 ± 0.5	20–21 20.7 ± 0.3	19–21 19.8 ± 0.5	19–22 20.9 ± 0.4	1.84	>0.05
F.c.	17–22 19.7 ± 1.5	18	16–20 18.5 ± 0.6	16–22 18.7 ± 1.8	17–22 19.3 ± 1.1	16–22 18.6 ± 0.6	0.58	>0.05
ZZ	118–160 139.3 ± 12.1	111	105–126 116.2 ± 3.3	108–115 111.5 ± 3.5	111–160 132.3 ± 11.1	105–126 114.9 ± 2.6	1.98	>0.05
Lor	7–12 9.3 ± 1.5	8	6–11 8.5 ± 0.9	7–11 9 ± 1.2	7–12 9 ± 1.1	6–11 8.7 ± 0.7	0.27125	>0.05

Notes: Statistically significant differences are highlighted in bold.

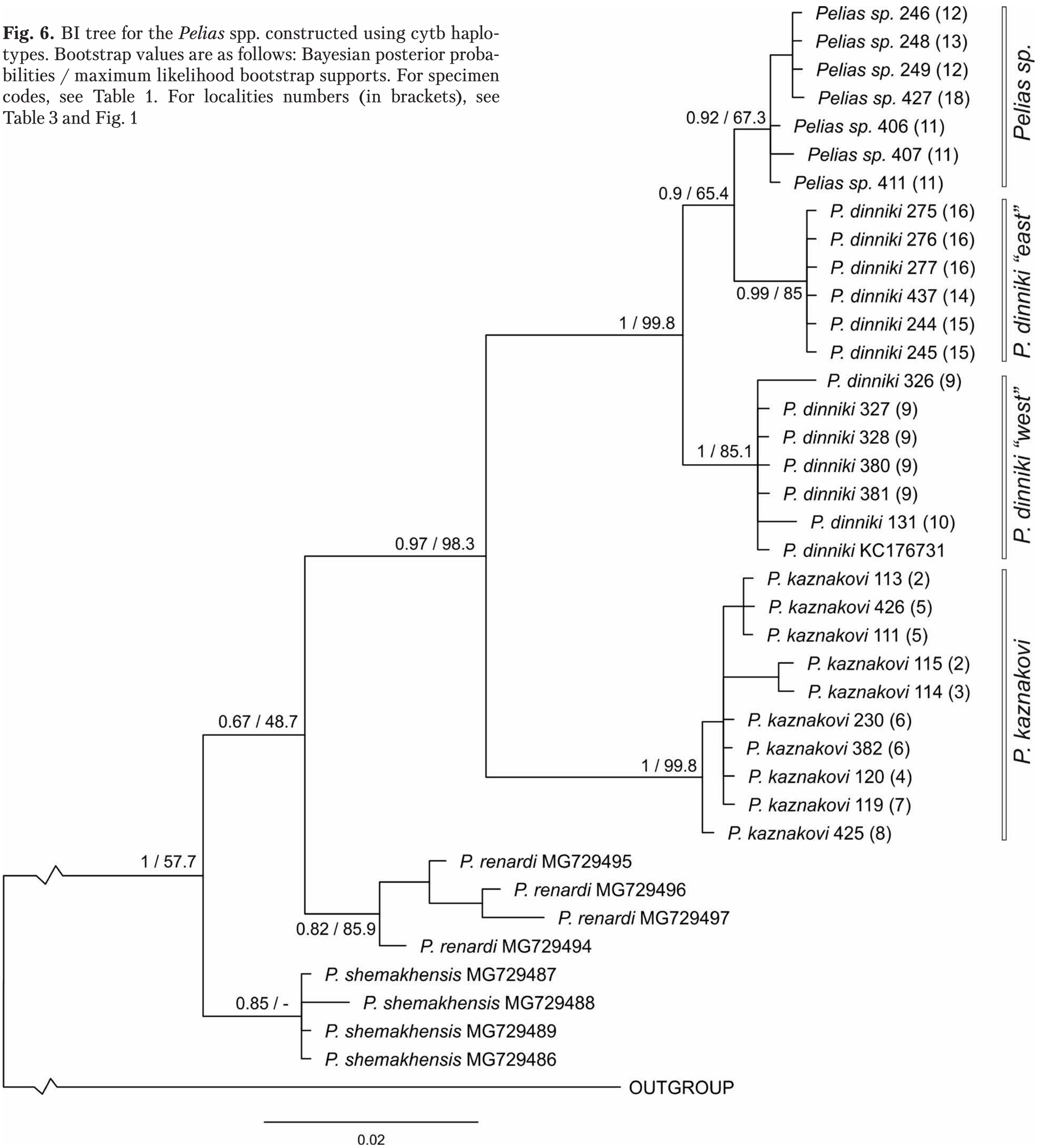
Table 5. Comparison of morphological characters of adult and juvenile specimens of *Pelias kaznakovi* from KT – Ab. See Table 2 for abbreviations

Character	♂♂ Adult (n = 10) Min–max X̄±m	♂♂ Juv. (n = 24) min–max X̄±m	♀♀ Adult (n = 15) min–max X̄±m	♀♀ Juv. (n = 17) min–max X̄±m	♂♂ Adult + Juv. (n = 34) min–max X̄±m	♀♀ Adult + Juv. (n = 33) min–max X̄±m	t	p
T.l.	382–510 443 ± 16.6	159–283 193.3 ± 5.7	390–550 467.4 ± 10.8	154–293 196.5 ± 10.2	–	–	–	–
SVL	322–438 377.4 ± 14.6	137–243 166.2 ± 5	347–485 415.9 ± 9.1	134–261 174.2 ± 9.3	–	–	–	–
L.cd	54–75 65.6 ± 2.6	22–40 27.1 ± 0.8	43–65 52.3 ± 1.7	17–32 22.3 ± 1	–	–	–	–
Pil	11.3–15.5 13.5 ± 0.4	7.3–10.9 8.9 ± 0.2	10–16.5 13.4 ± 0.4	7–10.6 8.7 ± 0.3	–	–	–	–
L.c.	19.1–26 22.5 ± 0.8	12–17.7 13.4 ± 0.3	20.7–28.2 24.6 ± 0.6	11.8–19 14.2 ± 0.5	–	–	–	–
Lt.c.	11.3–16.3 13.8 ± 0.5	6.6–11.3 8.6 ± 0.2	13–19.4 15.5 ± 0.5	6.1–12.1 8.9 ± 0.4	–	–	–	–
Al.c	6.3–10.3 8.5 ± 0.4	4.2–7.8 5.2 ± 0.2	7–11.9 9.4 ± 0.3	4.1–8.3 5.6 ± 0.3	–	–	–	–
R	47.3–73.7 61.6 ± 2.6	48.4–86.1 62.4 ± 2	46.8–72.9 61.2 ± 1.9	52.5–73.9 62.3 ± 1.7	–	–	–	–
Pr	1–5 2.4 ± 0.4	1–3 2 ± 0.1	0–4 2.1 ± 0.3	1–3 1.8 ± 0.2	1–5 2.1 ± 0.2	0–4 1.9 ± 0.2	0.93	>0.05
Ven	127–135 131.2 ± 0.7	126–136 131.3 ± 0.6	130–142 135.4 ± 1	125–145 135.1 ± 1.2	126–136 131.2 ± 0.4	125–145 135.3 ± 0.8	**4.66**	<0.001
S.cd.	31–40 36 ± 0.8	31–42 35.3 ± 0.6	22–33 27.3 ± 0.7	20–36 27.1 ± 1	31–42 35.5 ± 0.5	20–36 27.2 ± 0.6	**10.80**	<0.001
Ap	1–2 1.6 ± 0.2	1–2 1.7 ± 0.1	1–2 1.5 ± 0.1	1–2 1.3 ± 0.1	1–2 1.6 ± 0.1	1–2 1.4 ± 0.1	1.99	>0.05
C.s.	6–17 11 ± 1.1	4–18 8.9 ± 0.7	5–20 10.5 ± 0.9	4–15 8.8 ± 0.7	4–18 9.5 ± 0.6	4–20 9.6 ± 0.6	0.07	>0.05
Can	5–6 5.6 ± 0.2	5–6 5.7 ± 0.1	5–8 5.7 ± 0.2	5–6 5.3 ± 0.1	5–6 5.6 ± 0.1	5–8 5.5 ± 0.1	1.02	
Sq1	21–23 21.7 ± 0.3	21–25 22.3 ± 0.3	20–26 22.2 ± 0.5	21–24 22.5 ± 0.3	21–25 22.1 ± 0.2	20–26 22.3 ± 0.3	0.66	>0.05
Sq2	21–21 21 ± 0	21–23 21.2 ± 0.1	21–22 21.1 ± 0.1	21–23 21.4 ± 0.2	21–23 21.1 ± 0.1	21–23 21.2 ± 0.1	0.55	>0.05
Sq3	16–18 17 ± 0.2	17–19 17.2 ± 0.1	17–19 17.1 ± 0.1	17–19 17.3 ± 0.2	16–19 17.2 ± 0.1	17–19 17.2 ± 0.1	0.48	>0.05
Supralab	17–21 18.6 ± 0.4	16–20 18.2 ± 0.2	17–22 19.2 ± 0.5	17–20 18.2 ± 0.2	16–21 18.3 ± 0.2	17–22 18.7 ± 0.3	1.15	>0.05
Sublab	20–26 21.5 ± 0.6	18–24 21.2 ± 0.3	20–22 21.3 ± 0.2	18–23 20.9 ± 0.3	18–26 21.3 ± 0.3	18–23 21.1 ± 0.2	0.59	>0.05
F.c.	18–26 21.7 ± 0.7	20–24 21.4 ± 0.2	17–25 21.1 ± 0.5	16–24 20.5 ± 0.5	18–26 21.5 ± 0.3	16–25 20.8 ± 0.3	1.63	>0.05
ZZ	110–152 128.5 ± 6.5	113–153 130.7 ± 2.9	111–147 129.2 ± 5.8	112–129 120.6 ± 1.6	110–153 130.1 ± 2.7	111–147 123.5 ± 2.3	1.76	>0.05
Lor	9–15 11.4 ± 0.5	7–16 10.6 ± 0.5	8–17 11.7 ± 0.6	6–14 10.5 ± 0.6	7–16 10.9 ± 0.4	6–17 11 ± 0.4	0.31	>0.05

Notes: Statistically significant differences are highlighted in bold.

samples in the CDA was estimated as the value of the Makhalonobis distance (Tyurin et al. 2003). The distances between the centers of the samples of the males of vipers varied from 18.7 to 24.4. They were roughly equal between males of *P. dinniki* and *Pelias sp.* (18.7), as well as *P. kaznakovi* and *P. dinniki* (18.9); the maximal value was between *Pelias* sp. and *P. kaznakovi* (24.4) (Table 12). In females, these distances between the centers of the samples varied from 17.7 to 30.8. The minimum (17.7) distance was

Fig. 6. BI tree for the *Pelias* spp. constructed using cytb haplotypes. Bootstrap values are as follows: Bayesian posterior probabilities / maximum likelihood bootstrap supports. For specimen codes, see Table 1. For localities numbers (in brackets), see Table 3 and Fig. 1



recorded between the females of *Pelias sp.* and *P. kaznakovi*; the maximal distances between the females of *P. kaznakovi* and *Pelias dinniki* (24.0) as well as *P. dinniki* and *Pelias sp.* (30.8) (Table 13).

The contribution of different morphological characters to discrimination of groups was different. Since the maximal percentage of variance is taken into account by the first discriminant function, and it is for this function that animals were divided into main groups, we describe the contribution of traits to the separation of groups based on the values of this function. Because the first discriminant function takes into account the most percent of dispersion and the dividing of animals into basic groups occurs exactly along it, we describe the contribution of characters to the division of groups based on the values of this function (Tables 14 and 15).

The followings characters made the maximal contribution to discrimination of the groups of the males (Table 14): canthals, wings of zigzag (ZZ), loreals, subcaudals, apicals, supralabials, number of shields around the eyes, preventrals.

The followings characters made the maximal contribution to discrimination of the groups of the females (Table 15): wings of zigzag (ZZ), canthals, number of scales around the posterior part of body (Sq3), loreals, apicals, sublabials, crown scales.

During our study, new information was obtained about the morphological characters and geographical variability of the shield-head vipers of the "*kaznakovi*" complex from the western part of the Caucasian Ecoregion. Substantial differences in the mean values of numeral and meristic characters of the vipers from the left bank basin of the middle flow of the Kura River were most valuable (Table 3 and 4) in comparison with *Pelias kaznakovi* from KT – Ab (including the type location) (Table 9–10). The discrimination of the six groups from three samples, selected on the principle of geographical and sexual identity using the cluster analysis and CDA (Figs 4, 5; Tables 12, 13) is also significant.

2. Genetic analysis

Based on the results of the analysis of the mitochondrial cytochrome *b* gene (Fig. 6), the new species forms a separate cluster, not sister to *Pelias kaznakovi*. *P. kaznakovi* takes a separate position, sister to *P. dinniki*, and *Pelias* sp. from the left-bank basin of the middle flow of the Kura River falls into a cluster that combines Western and Eastern *P. dinniki* with the maximum support. They grouped, although with not with a very high support, with Eastern *P. dinniki*.

Genetic distances, according to the criteria proposed by Freitas et al. (2020), were minimal between Eastern and Western *Pelias dinniki* and *Pelias* sp. (0.9% and 1.7%, respectively) and significant between *P. kaznakovi* and *Pelias* sp. (4.7%) and between *Pelias* sp. and *P. renardi* (5.6%) (Table 16).

SYSTEMATICS

The results obtained on morphology, genetics and ecology of the studied vipers suggest taxonomic validity of vipers from the left bank basin of the middle flow of the Kura River in Eastern Ge and SO.

Family Viperidae Laurenti, 1768

Genus *Pelias* Merrem, 1820

Pelias tuniyevi Ananjeva, Gabaev, Iremashvili, Lotiev, Petrova sp. nov.

Holotype. SNP No 937, adult male, SO, Znaur District, vicinity of Kharisdzhin V. (=Tormaneuli V.), 42.2504°N, 43.8398°E, 1010 m above sea level, 14.05.2014, collector G. Khasity (Fig. 7).

Paratypes. Twelve specimens: SNP 1054 (1 adult female and 1 juvenile male, 7 born in terrarium), Ge, Shida-Kartlis Territory, Khashuri District, Tashiskari V., 41.5704°N, 43.3010°E, 720 m asl, 09.2015, Coll. Z. Khachidze; 936 (adult male), SO, Kharisdzhin V., 23.04.2014, Coll. G. Khasity; 915 (adult male), SO, Tskhinval District, vicinity



Fig. 7. Holotype of *Pelias tuniyevi* sp. nov. (SNP No 937) (photo B.S. Tuniyev)

Table 6. Sexual dimorphism of adult specimens of *Pelias tuniyevi* sp.nov. from SO – Ge. See Table 2 for abbreviations

Character	♂♂ (n = 3) min–max X̄±m	♀♀ (n = 6) min–max X̄±m	t	P
T.l.	382–471 421.3 ± 26.2	327–466 412.5 ± 20.2	0.26	>0.05
SVL	330–401 365.3 ± 20.5	297–425 371.7 ± 18.4	0.21	>0.05
L.cd	46–70 56 ± 7.2	30–46 40.8 ± 2.4	2.59	<0.05
Pil	12–13.4 12.5 ± 0.5	10.6–13.2 12 ± 0.5	0.69	>0.05
L.c.	20.7–22.9 21.5 ± 0.7	20.3–22.7 21.6 ± 0.4	0.15	>0.05
Lt.c.	11.3–12.3 11.8 ± 0.3	11.1–14.4 12.5 ± 0.5	0.85	>0.05
Al.c	7.9–9.3 8.6 ± 0.4	7–10 8.5 ± 0.5	0.21	>0.05
R	69.9–75.6 72.6 ± 1.7	56.9–90.1 68.3 ± 5.1	0.56	>0.05
Pr	2–3 2.7 ± 0.3	1–4 2.3 ± 0.4	0.51	>0.05
Ven	128–131 129.7 ± 0.9	129–136 132 ± 1	1.441	>0.05
S.cd.	28–36 33 ± 2.5	23–28 24.8 ± 0.7	4.20	<0.01
Ap	1–2 1.3 ± 0.3	1–2 1.3 ± 0.2	0.00	>0.05
C.s.	5–14 8.7 ± 2.7	4–9 7.2 ± 0.8	0.70	>0.05
Can	5–7 6 ± 0.6	5–7 5.7 ± 0.3	0.54	>0.05
Sq1	21–23 21.7 ± 0.7	20–22 20.8 ± 0.3	1.33	>0.05
Sq2	21–22 21.3 ± 0.3	19–21 20.7 ± 0.3	1.25	>0.05
Sq3	17–19 17.7 ± 0.7	16–17 16.8 ± 0.2	1.67	>0.05
Supralab	16–19 17.7 ± 0.9	18–19 18.3 ± 0.2	1.01	>0.05
Sublab	19–21 19.7 ± 0.7	19–22 21 ± 0.5	1.53	>0.05
F.c.	17–22 19.7 ± 1.5	16–20 18.5 ± 0.6	0.92	>0.05
ZZ	118–160 139.3 ± 12.1	105–126 116.2 ± 3.3	2.33	>0.05
Lor	7–12 9.3 ± 1.5	6–11 8.5 ± 0.9	0.52	>0.05

Notes: Statistically significant differences are highlighted in bold.



Fig. 8. Paratypes of *Pelias tuniyevi* sp. nov.: A – Uanat V. (1935) (photo B.S. Tuniyev); B – Atsriskhevi V. (1086) (photo V.V. Tikhonov); C – Kharisdzhin V. (1182) (photo B.S. Tuniyev); D – Kharisdzhin V. (951) (photo B.S. Tuniyev); E – Tashiskari V. (1140); F – Tashiskari V. (1054)

of Atsriskhevi V., 42.2970°N, 44.2238°E, 1325 m asl, 23.09.2012, Coll. E.E. Komarov; 1182 (adult female) (the same as holotype); 1140 (adult female), Ge, Tashiskari V., 22.10.2017, Coll. G.N. Iremashvili; 1086 (adult female), vicinity of Atsriskhevi V., 18.08.2016, Coll. V.V. Tikhonov; 951 (adult female), Kharisdzhin V., 14.05.2014, Coll. G. Khasity; 1935 (adult female), SO, Tskhinval District, vicinity of Uanat V. (=Vanati V.), 42.2867°N, 44.0535°E, 1013 m asl, 03.09.2018, Coll. Ch.B. Bukulov; 1095 (juvenile

Table 7. Sexual dimorphism of adult specimens of *Pelias kaznakovi* from KT – Ab. See Table 2 for abbreviations

Character	♂♂ (n = 10) min–max $\bar{X}\pm m$	♀♀ (n = 15) min–max $\bar{X}\pm m$	t	P
T.l.	382–510 443 ± 16.6	390–550 467.4 ± 10.8	1.29	>0.05
SVL	322–438 377.4 ± 14.6	347–485 415.9 ± 9.1	2.37	<0.05
L.cd	54–75 65.6 ± 2.6	43–65 52.3 ± 1.7	4.56	<0.001
Pil	11.3–15.5 13.5 ± 0.4	10–16.5 13.4 ± 0.4	1.25	>0.05
L.c.	19.1–26 22.5 ± 0.8	20.7–28.2 24.6 ± 0.6	2.16	<0.05
Lt.c.	11.3–16.3 13.8 ± 0.5	13–19.4 15.5 ± 0.5	2.19	<0.05
Al.c	6.3–10.3 8.5 ± 0.4	7–11.9 9.4 ± 0.3	1.68	>0.05
R	47.3–73.7 61.6 ± 2.6	46.8–72.9 61.2 ± 1.9	0.13	>0.05
Pr	1–5 2.4 ± 0.4	0–4 2.1 ± 0.3	0.72	>0.05
Ven	127–135 131.2 ± 0.7	130–142 135.4 ± 1	3.11	<0.01
S.cd.	31–40 36 ± 0.8	22–33 27.3 ± 0.7	7.60	<0.001
Ap	1–2 1.6 ± 0.2	1–2 1.5 ± 0.1	0.32	>0.05
C.s.	6–17 11 ± 1.1	5–20 10.5 ± 0.9	0.38	>0.05
Can	5–6 5.6 ± 0.2	5–8 5.7 ± 0.2	0.46	>0.05
Sq1	21–23 21.7 ± 0.3	20–26 22.2 ± 0.5	0.82	>0.05
Sq2	21–21 21 ± 0	21–22 21.1 ± 0.1	0.81	>0.05
Sq3	16–18 17 ± 0.2	17–19 17.1 ± 0.1	0.62	>0.05
Supralab	17–21 18.6 ± 0.4	17–22 19.2 ± 0.5	0.88	>0.05
Sublab	20–26 21.5 ± 0.6	20–22 21.3 ± 0.2	0.29	>0.05
F.c.	18–26 21.7 ± 0.7	17–25 21.1 ± 0.5	0.75	>0.05
ZZ	110–152 128.5 ± 6.5	111–147 129.2 ± 5.8	0.08	>0.05
Lor	9–15 11.4 ± 0.5	8–17 11.7 ± 0.6	0.32	>0.05

Notes: Statistically significant differences are highlighted in bold.

female), vicinity of Atsriskhevi V., 07.09.2016, Coll. V.V. Tikhonov; 1079 (juvenile female), vicinity of Atsriskhevi V., 18.08.2016, Coll. V.V. Tikhonov; 930 (juvenile female), SO, Dzau District, Gufta V. (=Didi Gupta V. – Patara Gupta V.): 42.3592°N, 43.8892°E, 1060 m asl, 05.08.2019, Coll. V.N. Gabaev (Fig. 8A–F).

Diagnosis. Small-sized snake, males differ from all representatives of *Pelias kaznakovi* s.l. by minimal values of total length, length of pileus, width of head, numbers of ventral and subcaudal shields, and shields around eyes; females have minimal body length, length of pileus, width of head, number of shields around eyes and loreals, number of zigzag wings. The vipers of both sexes from the left-bank basin of the middle flow of the Kura River differ from all other compared vipers by small sizes and the minimum number of shields around the eyes. The dorsal surface of the males is beige-gray, yellowish-gray, rarely brownish-reddish, or yellow; the dorsal surface of the females is pinkish-gray, light brown, gray-yellow or melanistic. The majority of females has a weakly undulated zigzag pattern ranging in color from light- to dark-brown; the zigzag pattern of males is black or brown-black, with sharp wings and occasional interruptions. The throat in both sexes is light-colored, the belly is usually gray-spotted against a dark background; the lower part of the tail in both sexes is pinkish with varying numbers of dots in males and without dots in females.

Description of the holotype. Adult male having the following morphological characters: total length (T.l.) – 382 mm, length of tail (L. cd) – 52 mm; 3 preventrals; 128 ventrals; 35 subcaudals. The rostral and the preanals that lie on either side of the rostral come to the upper surface of the head, so that the rostral acts simultaneously as an apical shield, and the prenasals act as canthals; there are therefore 7 canthal shields. Length of pileus (Pil.) – 12.0 mm. Rostral index – 72.27. Crown shields (C.s.) – 14. The upper preocular shield is separated from the nasal (In.) by the upper loreal and posterior canthal shields on either side of the head. 21 rows of dorsal scales around the neck and at the midbody, and 19 at posterior part of the body, 21 sublabials in sum, 10 supralabials on the right and 9 on the left side 11/11 shields around eyes; 160 wings of zigzag, 6 loreals on either side. Length of the head – 20.8 mm, width – 11.9 mm, height – 8.6 mm. Frontal and parietal shields are not divided. Between the frontal and large upper oculars: 1 shield on the right and 2 on the left side. Supralabials are white, the 5 anterior ones on either side are thickly pigmented by small red-brown nettles, posteriors – without pigmentation, or contrasted two-color black-and-white. The holotype specimen is beige-grey from above, zigzag almost uninterrupted dark brown-black. The zigzag is connected to the dark W-shaped pattern of the head. The front part of the head is entirely black with gray edging of the upper oculars. On either side of the body is a row of large patches of the same color as the zigzag. Coloring of the throat is light; the belly is grey-spotted on a dark background, the lower part of the tail is dark spotted on a pinky background, the tip of the tail is light pink.

Description of the paratypes. The paratypes correspond to the description of the holotype with insignificant variations in size and meristic characters (Table 17). It should be noted that the female (No. 1086) from Atsriskhevi has a combination of pholidosis in the front of the head, with 7 canthals, similar to that of the holotype. Five paratypes have 2 apicals, four – 1 broad apical and two – 1 narrow apical. The majority of paratypes have 21 scales around the middle of body; two specimens have 19 and 22 scales, respectively. Upper preocular shield is separated from the nasal by the upper loreal in all paratypes.

Color patterns are very diverse. The main background of adults and young males is beige-gray, yellowish-gray, rarely brownish-reddish, or yellow; females – pinkish-gray, light brown, gray-yellow, and some specimens are melanistic. The zigzag in most females is wider than in the males, almost continuous, undulate, colored light brown, pink-brown, or dark brown, sometimes with dark brown wings; in the males the zigzag, regardless of width, has sharp wings, is black, or brown-black in color and sometimes disjunct. In young and semi-adult individuals, the zigzag is not different from the zigzag of adult animals, and the color is less bright. The color pattern of the pileus is more pronounced in males. On the sides of the body of the juveniles is a number of large spots of the same color as the zigzag that become even larger with age. Coloration of the throat is light in all specimens. The belly is grey-spotted on a dark background in most specimens, while the specimen from Uanat (1935) has a dark-spotted

Table 8. Sexual dimorphism of adult specimens of ***Pelias dinniki*** from West Caucasus. See Table 2 for abbreviations.

Character	♂♂ (n = 11) min–max $\bar{X}$±m	♀♀ (n = 24) min–max $\bar{X}$±m	t	P
T.l.	365–490 436.2 ± 12.8	373–523 445.4 ± 9.1	0.58	>0.05
SVL	314–428 379.9 ± 11.3	327–472 399.7 ± 8.2	1.37	>0.05
L.cd	46–65 56.3 ± 1.8	30–61 45.7 ± 1.6	3.94	<0.001
Pil	10.5–13.5 12.3 ± 0.3	10.9–13.8 12.4 ± 0.2	0.38	>0.05
L.c.	18.8–24.6 21.7 ± 0.5	13.5–25.7 21.9 ± 0.5	0.20	>0.05
Lt.c.	9.7–13.7 12 ± 0.4	10–14.2 12.5 ± 0.2	1.26	>0.05
Al.c	6.6–9.3 8.4 ± 0.2	6.6–9.8 8.2 ± 0.2	0.76	>0.05
R	63.2–87.4 70.8 ± 2.2	50–82.2 66 ± 1.6	1.73	>0.05
Pr	1–3 2.2 ± 0.2	1–3 2.3 ± 0.1	0.45	>0.05
Ven	130–136 132.5 ± 0.7	127–141 134.3 ± 0.6	1.72	>0.05
S.cd.	32–37 34.2 ± 0.7	24–32 28 ± 0.5	7.46	<0.001
Ap	1–2 1.4 ± 0.2	1–2 1.3 ± 0.1	0.67	>0.05
C.s.	6–14 10 ± 0.7	5–14 9.2 ± 0.5	0.99	>0.05
Can	5–6 5.4 ± 0.2	3–6 5.2 ± 0.1	0.90	>0.05
Sq1	18–23 21.3 ± 0.5	17–23 21.1 ± 0.3	0.28	>0.05
Sq2	19–21 20.5 ± 0.2	20–22 21 ± 0.1	2.32	<0.05
Sq3	16–19 17 ± 0.2	16–17 16.7 ± 0.1	1.39	>0.05
Supralab	16–18 17.1 ± 0.3	10–18 17.1 ± 0.4	0.01	>0.05
Sublab	18–22 20.4 ± 0.4	17–22 20 ± 0.3	0.86	>0.05
F.c.	18–23 20.2 ± 0.5	15–23 19.8 ± 0.4	0.56	>0.05
ZZ	137–208 160.5 ± 7.6	138–191 168.1 ± 3.6	1.00	>0.05
Lor	5–12 8.4 ± 0.6	7–12 9.4 ± 0.3	1.55	>0.05

Notes: Statistically significant differences are highlighted in bold.



Fig. 9. Known localities of *P. tuniyevi* sp. nov: Ge: 1. Baniskhevi Gorge; 2. Vicinity of Tashiskari V.; SO: 3. Vicinity of Kalet V.; 4. Vicinity of Kharisdzhin V. (terra typica); 5. Vicinity of Dodot V.; 6. Vicinity of Kusret V.; 7. Vicinity of Gufta V.; 8. Vicinity of Ksuis V.; 9. Vicinity of Atsriskhevi V.; 10. Vicinity of Uanat V.; 11. Vicinity of Artseu V.; 12. Vicinity of Grom V.; 13. Vicinity of Tbet V.; 14. Vicinity of Otreu V.

belly on a light background and in the specimen from Atsriskhevi (No. 1086) the belly is black. The lower part of the tail in both sexes is pinkish with varying degrees of dots in males and without dots in females. The coloration of the supralabials varies from almost white to black with different specks or stripes, which can be located both at the top of the shields and in the form of dark stripes at the seams.

Etymology. The species is named after Boris Tuniyev, who made a significant contribution to the study of the Caucasian herpetofauna and the taxonomy of the shield-head viper snakes.

Geographical distribution and biotopes. All known finds are located in the left-bank basin of the middle flow of the Kura River from the Borzhom Gorge (east slope of Meskheti Ridge) in Ge to middle-mountain districts of SO (east foothills of Likhsky Ridge and south spurs of Central Caucasus). Known localities in Ge: vicinity of Tashiskari V. and Baniskhevi Gorge below Borzhomi; known localities in SO: Gufta V., vicinity of Kusret V. (=Kusreti V.), vicinity of Kotstykau V. (=Kverneti V.), vicinity of Uanat V. (=Vanati V.), vicinity of Otreu V. (=Otrevi V.), South-Ossetian Reserve – vicinity of ruins of Atsriskhevi V., vicinity of Artseu V. (=Artsevi V.), vicinity of Grom V. (=Gromi V.), vicinity of Kharisdzhin V. (=Tormaneuli V.), vicinity of Dodot V. (=Zemo-Dodoti V. – Kvemo-Dodoti V.), vicinity of Kalet V. (=Kaleti V.), vicinity of Ksuis V. (=Ksuisi V.), vicinity of Tbet V. (=Tbeti V.) (Fig. 9).

It inhabits mid-altitude broad-leaved forests, *Carpinus orientalis* shibliak and post-forest glades in the range of elevations from 700-850 m in the Borzhom Gorge of Ge, 800 m (Kalet V.) in SO to more than 1300 m asl (near the ruins of Atsriskhevi V., South Ossetian Reserve) (Fig. 10).

Table 9. Morphological characters of Pelias kaznakovi from Adzharo-Lazistan population (south-west Transcaucasia). See Table 2 for abbreviations.

Locality, collection No or literature source, sex, age	T.l.	SVL	L.cd.	Pil	L.c.	Lt.c.	Al.c	R	Pr	Ven	S.cd.	Ap	C.s.	Can	Sq2	Supralab	F.c.	ZZ	Lor
Mtirala SNP 1060, ♀ s.ad	360	325	35	11.0	20.6	11.2	8.2	73.2	2	136	24	2	6	6	23	20	19	108	6
Kintrish SNP 941, ♀ ad	508	450	58	14.4	27.3	20.0	9.8	49.0	2	134	27	1	11	5	21	16	20	-	14
Hopa (Baran et al., 2005) ♀ ad	489	430	59	-	-	-	-	-	-	138	24	1	-	-	21	14	19	-	-
Duzenli (Afsar, Afsar, 2009) ♀ ad	480	435	45	-	-	-	-	-	-	135	26	1	22	-	21	19	20	-	14
Kintrish 1141, ♂ ad	524	458	66	13.9	25.0	16.0	8.4	52.5	2	129	33	2	12	6	21	18	21	143	12
Findikli (Gül et al., 2016), ♂ ad	530	450	80	-	-	-	-	-	-	133	34	2	22	6	21	19	18	-	11
Borchka (Baran et al., 2005) ♂ ad	414	355	59	-	-	-	-	-	-	126	36	2	-	-	22	18	18	-	-
Efeler (Afsar, Afsar, 2009) ♂ s.ad	369	324	45	-	-	-	-	-	-	135	34	2	21	-	21	-	26	-	12
Camili (Afsar, Afsar, 2009) ♂ s.ad	-	-	50	-	-	-	-	-	-	-	35	2	17	-	21	18	18	-	9
Baltacik (Afsar, Afsar, 2009) ♂ ad	-	-	60	-	-	-	-	-	-	-	35	1	16	-	-	17	16	-	10



Fig. 10. Habitats of *P. tuniyevi* sp. nov.: A – *Carpinus orientalis* shibliak with forest glades in vicinity of Tashiskhari V. (photo B.S. Tuniyev); B – Derivates of broad-leaf forests and post-forest glades in vicinity of Kharisdzhin V. (terra typica) (photo B.S. Tuniyev).

Morphological, ecological and biogeographic notes

Geographically, the new species is isolated from the Adzharo-Lazistan population of *P. kaznakovi* by the medium-high Meskheti (Adzharo-Imeretinsky) Ridge (highest point – Mt. Mepitskaro, 2850 m) and its continuation, a rather low Likhsky (Suramsky) Ridge (Mt. Lokhoni, 1926 m).

There is every reason to assume that the ancestral form had a common geographic range in the southwestern Transcaucasia, which disintegrated into two populations in the Pleistocene and further fragmented in the basin of the Kura River in the Holocene, after the expansion of the xerophylous biota upward along the valley of the Kura River. Evidence for the Holocene expansion of xerophilous representatives of herpetofauna can still be seen today, for instance, in a recent find of *Dolichophis schmidii* (Nikolsky 1909) in SO (Tuniyev et al. 2017b). The valley of the Kura River, as a route of spreading of xerophylous herpetofauna, was considered by M.A. Bakradze (1977) based on the records of *Testudo graeca* L., 1758, *Lacerta media* (Lantz et Cyren, 1920), *Paralaudakia caucasia* (Eichwald 1831), *Eirenis modestus* Martin, 1838, *Hemorrhois ravergieri* (Menetries 1832), *Telescopus fallax iberus* Eichwald, 1831 in the Borzhom Gorge and upward. This conclusion is also supported by paleontological finds in Dmanisi and paleoclimatic reconstructions (Blain et al. 2014), indicating the presence in the early Pleistocene of semi-desert and steppe landscapes changing into Mediterranean light forest.

Despite the Holocene expansion of the xerophilous biota, many Colchian representatives of flora and fauna have survived in the Borzhom Gorge. Including the find of M.A. Bakradze (1969) *"P. kaznakovi"* made it possible to distinguish a special Borzhom refugium of the Colchian biota (Tuniyev 1990; 1997).

It is necessary to note the maximum size and a very bright color of *P. kaznakovi* from the Adzharo-Lazistan population (Fig. 11), compared to the KT – Ab population and, in fact, *P. tuniyevi* sp. nov. For a rather long time, characters of vipers such as less developed polymorphism and the absence of melanists in the southwestern Tanscaucasia, based on differences in allozyms (Nilson et al. 1995), were considered as characteristic for the northwestern cluster of the species range. We have also noted them for *P. tuniyevi* sp. nov. in SO too. In this regard, it is interesting to indicate the record of a melanistic female in the Kinthrish Reserve (941), which changes the prevailing concept and characterizes a single set of possible morphs in vipers in the canalization of evolutionary processes.

Differences are also noted in the structure of the hemipenis. *P. tuniyevi* sp. nov. has longitudinal rows of 2–3 large, identical sized and hook-shaped spikes replaced by a small number of small spikes in the distal part of the hemipenis (Fig. 12A). *P. kaznakovi* has longitudinal rows of 2–3 slightly curved large spikes, the longest of which occupy a proximal position, replaced in the distal part by a large number of small spikes, located in numerous rows and turned towards the furrow of the hemipenis (Fig. 12B). The hemipenis of *P. dinniki* is characterized by longitudinal

Table 10. Meristic characters in all age groups of *Pelias* spp. See Introduction and Table 2 for abbreviations

Character	SO – Ge Sample1		KT – Ab Sample 2		*Pelias dinniki* "west" Sample 3	
	♂♂ (n = 4) X̄±m	♀♀ (n = 9) X̄±m	♂♂ (n = 34) X̄±m	♀♀ (n = 32) X̄±m	♂♂ (n = 11) X̄±m	♀♀ (n = 24) X̄±m
Pr	2.3 ± 0.5	2.2 ± 0.3	2.1 ± 0.2	1.9 ± 0.2	2.2 ± 0.2	2.3 ± 0.1
Ven	129.3 ± 0.8	133.1 ± 1.2	131.2 ± 0.4	135.3 ± 0.8	132.5 ± 0.7	134.3 ± 0.6
S.cd.	31.8 ± 2.2	25.6 ± 0.8	35.5 ± 0.5	27.2 ± 0.6	34.2 ± 0.7	28 ± 0.5
Ap	1.3 ± 0.3	1.4 ± 0.2	1.6 ± 0.1	1.4 ± 0.1	1.4 ± 0.2	1.3 ± 0.1
C.s.	7.8 ± 2.1	8.3 ± 1	9.5 ± 0.6	9.6 ± 0.6	10 ± 0.7	9.2 ± 0.5
Can	5.8 ± 0.5	5.7 ± 0.2	5.6 ± 0.1	5.5 ± 0.1	5.4 ± 0.2	5.2 ± 0.1
Sq1	21.5 ± 0.5	21.3 ± 0.4	22.1 ± 0.2	22.3 ± 0.3	21.3 ± 0.5	21.1 ± 0.3
Sq2	21.3 ± 0.3	20.9 ± 0.3	21.1 ± 0.1	21.2 ± 0.1	20.5 ± 0.2	21 ± 0.1
Sq3	17.3 ± 0.6	16.9 ± 0.1	17.2 ± 0.1	17.2 ± 0.1	17 ± 0.2	16.7 ± 0.1
Supralab	18.3 ± 0.9	18 ± 0.3	18.3 ± 0.2	18.7 ± 0.3	17.1 ± 0.3	17.1 ± 0.4
Sublab	19.8 ± 0.5	20.9 ± 0.4	21.3 ± 0.3	21.1 ± 0.2	20.4 ± 0.4	20 ± 0.3
F.c.	19.3 ± 1.1	18.6 ± 0.6	21.5 ± 0.3	20.8 ± 0.3	20.2 ± 0.5	19.8 ± 0.4
ZZ	132.3 ± 11.1	114.9 ± 2.6	130.1 ± 2.7	123.5 ± 2.3	160.5 ± 7.6	168.1 ± 3.6
Lor	9 ± 1.1	8.7 ± 0.7	10.9 ± 0.4	11 ± 0.4	8.4 ± 0.6	9.4 ± 0.3

Table 11. Comparison of meristic features of all age groups (adults+juveniles) in studied samples of *Pelias* spp. See Table 2 for abbreviations

Character	♂♂ 1/2 n=38	♂♂ 1/3 n=15	♂♂ 2/3 n=45	♀♀ 1/2 n=41	♀♀ 1/3 n=33	♀♀ 2/3 n=56
Pr.	–	–	–	–	–	–
Ven.	*	*	–	–	–	–
S.c.	*	–	–	–	*	–
Ap.	–	–	–	–	–	–
C.s.	–	–	–	–	–	–
Can.	–	–	–	–	–	–
Sq.1	–	–	–	–	–	**
Sq.2	–	–	***	–	–	–
Sq.3	–	–	–	–	–	**
Supralab	–	–	***	–	–	**
Sublab	–	–	–	–	–	***
F.c.	**	–	*	**	–	–
ZZ	–	–	***	*	***	***
Lor.	–	–	**	*	–	**

Notes: sample 1 – SO – Ge; 2 – KT – Ab; 3 – *P. dinniki* "west"
* — p <0.05; ** — p <0.01; *** — p <0.001



Fig. 11. Color patterns of *P. kaznakovi* from Adzharo-Lazistan population: A, B – vicinity of Arkhavi, Turkey (photo B. Heras); C – Mt. Mtirala, Adzharia (photo B.S. Tuniyev), Ge; D – Vicinity of Batumi, Adzharia, Ge (photo B. Heras); E, F – Kintrish Reserve, Adzharia, Ge (F – photo B.S. Tuniyev).



Fig. 13. *Pelias shemakhensis kakhetiensis* from vicinity of Goridjvari V., Ge

rows of 2–3 large straight spikes, the largest of which are located in the medial part, and few small spikes (Fig. 12C).

In the Borzhom Gorge *P. tuniyevi* sp. nov. is sympatric, and in Tashiskari V. is syntopic with *Vipera transcaucasiana* Boulenger 1913, what is a larger and more competitive viper. Not so numerous as the latter, *P. tuniyevi* sp. nov. is found in small forest glades, overgrown shrubs and on the edge of the gorge with stony outcrops in the *Carpinus orientalis* shiblyak and in the Querceto-Carpinetum forest with a single *Picea orientalis* (Fig. 10A). The species is absent at talus slopes and large-block areas of the gorge where it is completely replaced by *V. transcaucasiana*.

A different situation is observed in the southern macro-slope of the Central Caucasus in the contact zone with the Inner Cartlian Plain. Given the modern find of G.N. Iremashvili *Pelias shemakhensis kakhetiensis* Tuniyev, Iremashvili, Petrova et Kravchenko, 2018 in Gorijvari V. (Fig. 13), there is vicariation of three species of shield-head vipers in various high-altitude ecological belts. *P. shemakhensis kakhetiensis* is found in the steppe biotopes of foothills along the valley of the Kura River. *P. tuniyevi* sp. nov. lives in the broad-leaved forest belt up to the lower boundary of the dark coniferous forests at the bottom of mid-altitude mountains, whereas the eastern form of *P. dinniki* is common in the subalpine mountain meadow belt.

It should be noted that the southern slope of the Great Caucasus in this area is very short and steep,

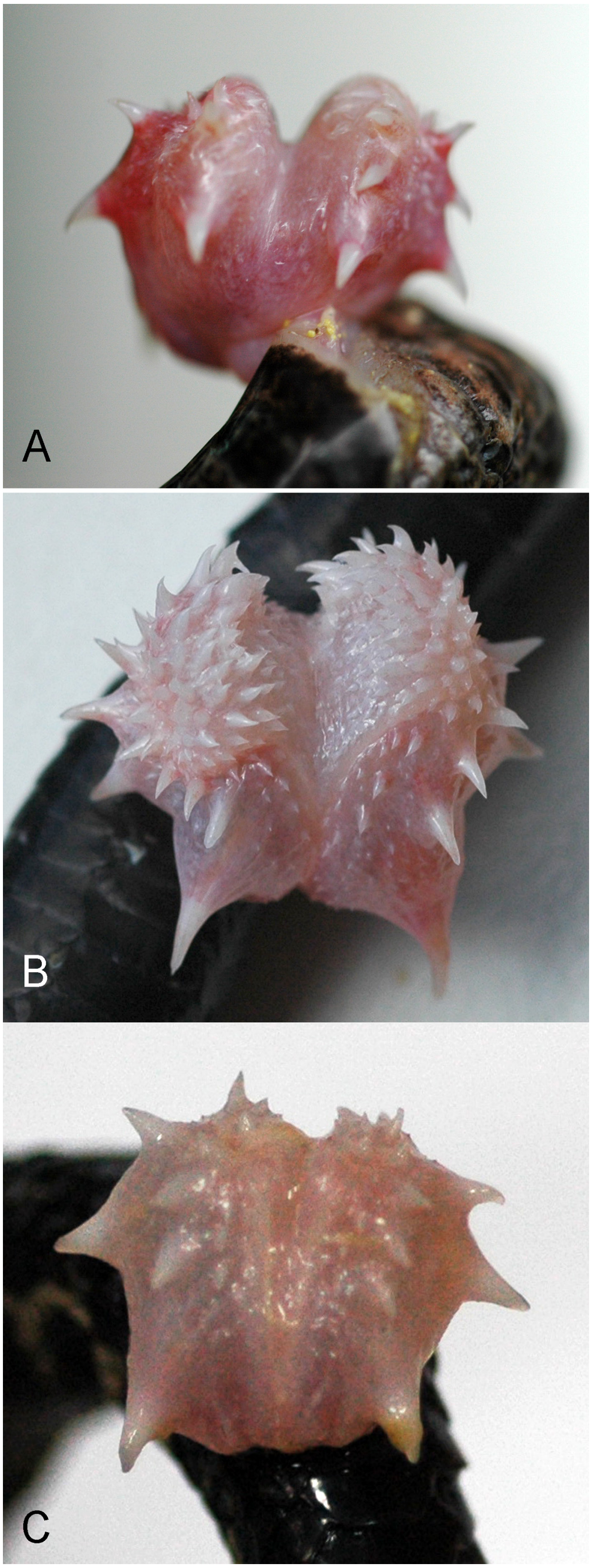


Fig. 12. Morphology of hemipenis (photo B.S. Tuniyev): A – *P. tuniyevi* sp. nov. (vicinity of Kharisdzhin Vil., SO, holotype), B – *P. kaznakovi* (Mt. Soutlyantepe, Sochi, Russia), C – *P. dinniki* (beginning of Malaya Laba River, Caucasian Reserve, Russia, topotype).

Table 12. Mahalonobis distances (right) and significance (left) levels between samples of males of *Pelias dinniki*, *P. tuniyevi* and *P. kaznakovi*, according to CDA results. See Table 1 for average values of the samples.

Sample	*P. dinniki* "west"	*P. tuniyevi*	*P. kaznakovi*
P. dinniki west	–	18.67837	18.86554
P. tuniyevi	0.042662	–	24.40798
P. kaznakovi	0.000280	0.004819	–

Table 13. Mahalonobis distances (right) and significance levels (left) between samples of females of *Pelias dinniki* "west", *P. tuniyevi*, and *P. kaznakovi*, according to CDA results. See Table 1 for average values of the samples.

Sample	*P. dinniki* "west"	*P. tuniyevi*	*P. kaznakovi*
P. dinniki west	–	30.79607	23.98708
P. tuniyevi	0.000044	–	17.73442
P. kaznakovi	0.000008	0.002592	–

Table 14. Contribution of different morphological characters in separation of males of *Pelias dinniki* "west", *P. tuniyevi*, and *P. kaznakovi*, according to CDA results. See Table 2 for abbreviations.

Character	Standardized coefficient of the first discriminant function	Character rank
Pr	0.37	8
Ven	0.13	13
S.cd.	0.65	4
Ap	0.63	7
C.s.	0.22	10
Can	1.25	1
Sq1	0.10	14
Sq2	0.18	12
Sq3	0.33	9
Supralab	0.59	5
Sublab	0.19	11
F.c.	0.50	6
ZZ	0.95	2
Lor	0.81	3

Table 15. Contribution of different morphological characters in separation of females of *Pelias dinniki* "west", *P. tuniyevi*, and *P. kaznakovi*, according to CDA results. See Table 2 for abbreviations

Character	Standardized coefficient of the first discriminant function	Character rank
Pr	0.06	13
Ven	0.09	12
S.cd.	0.01	14
Ap	0.23	5
C.s.	0.19	7
Can	0.45	2
Sq1	0.13	10
Sq2	0.19	8
Sq3	0.33	3
Supralab	0.18	9
Sublab	0.22	6
F.c.	0.13	11
ZZ	0.92	1
Lor	0.28	4

Table 16. Uncorrected p-distances between samples of *Pelias* spp.

Samples	*P. tuniyevi* sp.n.	*P. kaznakovi*	*P. renardi*	*P. dinniki* "west"	*P. dinniki* "east"
P. tuniyevi sp. n.	0.001				
P. kaznakovi	0.047	0.003			
P. renardi	0.056	0.046	0.008		
P. dinniki (west)	0.017	0.053	0.060	0.004	
P. dinniki (east)	0.009	0.048	0.055	0.019	0.000

almost without advanced ridges. Thus, ideal conditions were created for unhindered contacts in the condition of multiple movements of high-altitude belts in the Pleistocene and Holocene. *P. tuniyevi* sp. nov. could have repeatedly come into contact with two other species and formed hybrids. Apparently, the observed sharp zigzag wings and gray tones in some males of *P. tuniyevi* sp. nov. are the result of gene introgression as a consequence of the past hybridization, at least with eastern *P. dinniki*. This is also indicated by the fact that *P. tuniyevi* sp. nov. and eastern *P. dinniki* belong to the same cluster, while retaining some external characters bringing *P. tuniyevi* sp. nov. closer to *P. kaznakovi*, and is further supported by the results of the cluster analysis and for females also of the CDA analysis. As opposed to the observed morphological similarity of *P. tuniyevi* sp. nov. with *P. kaznakovi* and clear differences in ecology from *P. dinniki*, genetic distances (Table 16) were significant between *P. kaznakovi* and *P. tuniyevi*

Table 17. Morphological characters of the type series of *Pelias tuniyevi* sp. n.

N	Catalogue number	Sex	T.l.	SVL	L.cd.	Pr.	Ven.	S.c.	Ap.	R	Pil.	C.s.	Can.	Sq.1	Sq.2	Sq.3	Supr.	Sublab	F.c.	ZZ	Lor.	L.c.	Lt.c.	Al.c.
1	1054 juv	male	156	136	20	1	128	28	1	59.76	8.8	5	5	21	21	16	20	20	18	111	8	13.0	8.2	4.9
2	937* ad.	male	382	330	52	3	128	35	1	72.27	12.0	14	7	21	21	19	19	21	22	160	12	20.8	11.9	8.6
3	936 ad.	male	411	365	46	3	131	28	2	69.91	12.1	7	6	21	21	17	16	19	20	118	9	20.7	11.3	7.9
4	915 ad.	male	471	401	70	2	130	36	1	75.61	13.4	5	5	23	22	17	18	19	17	140	7	22.9	12.3	9.3
5	1182 ad.	female	419	376	43	3	134	25	2	69.91	12.7	6	6	20	21	17	19	22	18	126	6	22.7	11.3	7.9
6	1140 ad.	female	327	297	30	1	131	23	1	56.91	10.7	4	5	20	21	16	18	20	16	116	6	21.0	12.3	7.0
7	1086 ad.	female	466	425	41	2	136	24	1	73.39	13.0	8	7	21	21	17	18	19	20	–	8	22.2	12.4	9.1
8	1054 ad.	female	456	410	46	2	131	25	1	62.5	13.2	7	5	21	21	17	18	22	19	117	10	22.7	14.4	9.0
9	951 ad.	female	400	360	40	4	131	24	2	57.04	10.6	9	6	22	21	17	18	21	19	117	10	20.3	13.5	7.7
10	1935 ad.	female	407	362	45	2	129	28	1	90.09	11.7	9	5	21	19	17	19	22	19	105	11	20.6	11.1	10.0
11	1095 juv.	female	195	175	20	1	139	25	2	65.79	7.7	6	6	21	21	17	16	20	18	108	7	13.4	7.6	5.0
12	1079 juv.	female	171	149	22	3	130	31	1	68.42	8.6	12	5	23	21	17	18	21	22	115	9	13.5	7.6	5.2
13	930 juv.	female	205	185	20	2	137	25	2	71.87	9.7	14	6	23	22	17	18	21	16	-	11	16.2	9.6	6.9

Note: * – holotype.

sp. nov. (4.7%), but minimal between eastern *P. dinniki* and *P. tuniyevi* sp. nov. (0.9%).

Currently, biotopes of *P. tuniyevi* sp. nov. are characterized by more xero-mesophilic traits and moderately warm mezo-climate than typical mesophilic biotopes of North-Colchian (KT – Ab) and, especially, Adzharo-Lazistanian *P. kaznakovi*, living in the humid subtropical climate.

The conflict between morphological and genetic analysis is known for many groups of reptiles and continues to be the subject of debate (Pavlinov 2014; Tuniyev et al. 2014; Ananjeva 2019; Speybroeck et al. 2020). The categorical conclusions of a number of authors (Gvozdik et al. 2012; Zinenko et al. 2015) based solely on the results of the genetic analysis are, in our opinion, a priori assumptions, especially in the case of well-developed geographical and hypsometric isolation, with objective differences in external morphology (size, coloration and color pattern, pholidosis). These features are unique for each species (subspecies) and associated with ecological characteristics of biotopes, geographic distribution and the history of speciation, with the accumulation of original features in each region of formation. It should be taken into account an essential role of hybrid speciation, which have probably occurred in vipers throughout the Caucasus (Joger and Zinenko 2021). We confirm the need to implement integrative taxonomic approaches for the recognition of evidence-based taxonomic units in Eurasian vipers and further research to clarify taxonomic arrangements (Freitas et al. 2020), which is important for the study and conservation of this important model group of the Caucasian Ecoregion.

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